PREVERNAL LEAFING OF ASPEN IN UTAH MOUNTAINS

WALTER P. COTTAM

With two plates

THE ROCKY MOUNTAIN ASPEN (*Populus tremuloides Michx., var. aurea* Tidestrom) dominates more mountainous terrain in Utah at elevations between 7,000 and 10,000 feet than any other forest species. Several features of its growth-form, together with its peculiar autecology and synecology, make this species a very conspicuous forest type. Unlike all other prominent forest species with which it may be associated, such as Douglas fir, white fir, alpine fir, blue spruce, Engelmann spruce, ponderosa pine and lodgepole pine, the aspen is deciduous in habit.

Often the aspen occurs in almost pure stands, which may vary in size from a few square rods to several square miles of solid forest. But whether small or large, the aspen stands are sharply discontinuous, single aged and usually dense. The shiny green leaves of summer, the multi-colored shades of yellow in autumn, and the slender, straight, white boles at all seasons of the year are features of the aspen that set it apart in contrast to all contiguous association types, whether mountain conifers or browse.

But the contrast that exists between the aspen stands and other mountain vegetation types is often exceeded, in early spring at least, by striking differences in the time of leafing within the aspen groves themselves. This phenomenon is widespread throughout the mountains of Utah and neighboring states. In early spring almost any aspen forest shows sharply discontinuous colonies of trees that attain full leaf two or three weeks earlier than the major surrounding stand in which at any other time they are likely to remain unnoticed except by the critical observer.

At mid-elevations these colonies of prevernal aspen are usually small in comparison with the forest as a whole, and their outline is variable. Frequently they assume a circular shape, but they may be seen as a narrow, serpentine band bisecting large groves. In general, the position of these prevernal colonies seems to have no correlation with slope, exposure, soil, altitude, or sex of trees, but wherever they occur or whatever shape they may assume, the line that separates them from the retarded major population of trees is sharp, and rarely do the two forms intermingle as individuals.

CONTROLS OF PREVERNAL LEAFING

For years the author has been intrigued with the causes underlying the prevernal leafing of aspen colonies and surprised at the lack of text-book reference to this phenomenon. But few facts of aspen ecology

escaped the critical eye and pen of F. S. Baker, who in 1921 wrote an excellent description of the prevernal leafing of aspen colonies with special reference to the Wasatch Plateau of central Utah. His paper (4), entitled "Two Races of Aspen," points out certain taxonomic differences between early- and late-leafing stands and concludes: "The writer confesses an entire inability to explain the causes of these two widely distributed and closely intermingled races of aspen." Yet throughout the article Baker implies that the causes, whatever they may be, are genetic and never environmental.

There can be little doubt that at least two and probably several races of aspen exist that show striking differences in time of leafing. Evidence of these strains is seen in the variable combinations of certain morphological characters often associated with the physiological functions that regulate leafing response. These morphological characters are sufficiently distinct and constant as to enable one to distinguish the races at the seasons of the year when leaf color and size no longer offer safe clues to their identity. For example, Baker pointed out that in the Wasatch Plateau area boles of the early variety are yellow-green in color in contrast to the powdery-white appearance of the late-leafing variety. The writer has found no exception to this phenomenon throughout the northern half of Utah. This bole color difference is due to the failure of the early-leafing form to produce the usual copious bloom on the bark exterior characteristic of the late-leafing variety.

Another character generally useful in distinguishing the leafing strains of aspen is the pruning habit of the trees. In central and northern Utah, early-leafing aspens in general fail to prune themselves of the lower, small, dead branches on the trunk, thereby presenting an appearance of low vigor and untidiness entirely foreign to the late-leafing strain. (Careful observation, however, discloses that this lack of vigor is more apparent than real.)

Thus, in central and northern Utah, prevernal leafing of aspen is associated with the apparently genetic characters of yellow boles and poor pruning. However, on the Aquarius Plateau of south central Utah, the early-leafing character is associated with white boles and clean pruning, while the late-leafing trees are yellow-boled, non-pruning, a complete reversal of genetic alignment of the northern form.

In distribution within the aspen belt, early-leafing varieties dominate the higher elevations only. At the upper limits of the belt, aspens exist mainly as dwarfed thickets, which are always of the early-leafing forms as distinguished, of course, by the bole color and pruning habit. Conversely, the lower limits of the aspen belt are dominated by late-leafing varieties. Thus the contrast between early- and late-leafing aspens is most pronounced in the spring at mid-elevations, where the two forms are often intermingled as colonies. Here also is found the greatest contrast in autumn, for the early-leafing forms, as a rule, maintain their green color several days longer in the fall than do the late-leafing varieties.

For several years the writer has observed a few areas where contiguous colonies of early- and late-leafing aspen fail to present the morphological

differences mentioned above. In all of these exceptions the boles of both aspen groups are white and well pruned, yet the length of the leafing time differences is the usual two to three weeks. One such area is located at the head of South Willow Creek Canyon in the Stansbury Mountains, approximately fifty miles west of Salt Lake City. Another is found in the Abajo Mountains west of Monticello in southeastern Utah. Both areas occur at an elevation of about 7,500 feet.

TEMPERATURE CONTROLS OF PREVERNAL LEAFING

The Stansbury group appears at the bottom of an east-west canyon at a point where the generally straight canyon forks abruptly. The major fork heads south and in a circuitous manner drains the summit of the 10,000 foot range. The minor fork proceeds west for approximately one mile where it ends more or less abruptly, forming a sort of "boxed" segment rather well protected from air drainage from the summit above. Each spring in late May, aspens in this box canyon may be seen in almost full leaf with a sharp line scarcely more than a rod wide bisecting the grove and separating those in leaf from a half mile area of leafless aspens lying at and below the confluence of the major south fork.

Here there is an anomalous condition in which a grove of aspens leaf out considerably before their neighbors two to three hundred feet below them in elevation. In order to ascertain whether temperature might be a controlling factor in this phenomenon, a transect of four stations (two above and two below the leafing line) was established. Recording thermographs, fastened to the aspen branches ten feet above the ground and protected by white canvas tents, were used in this preliminary experiment, as well as in others to be reported below. Readings were begun May 7 and terminated May 19, 1951. During this period neither group of aspen had progressed beyond the swollen bud stage. Figure I shows the daily minimum, maximum and mean temperatures in both aspen groups over this period of 13 days.

The comparative summaries given in Figure I leave little doubt that these two major stands of aspen, showing marked differences in the time of leafing, exist under strict temperature controls and are not separate races. Considering the fact that the early-leafing aspen while occupying the higher elevations show a daily mean temperature two to three degrees greater than the late-leafing stands, these temperature differences seem highly significant. Translated into altitudinal effects, the temperature difference between these two aspen groups is equivalent to approximately 1000 feet in elevation. Furthermore, observations in this area in early June, 1951, disclosed several typical prevernal colonies of genetically controlled aspen within the major retarded zone of lower temperature. These small isolated colonies of yellow-boled aspen came into leaf at approximately the same time as the large stand of white-boled aspen of the higher temperature area.

GENETIC CONTROLS OF PREVERNAL LEAFING

Circumstances prevented the writer from visiting the prevernal leafing aspen colonies of the Abajo Mountains of southeastern Utah until August, 1951. With the aid of kodachrome pictures taken in May, 1950, the exact position of these colonies was ascertained. Comparative temperature records were taken for a period of four days. No significant temperature differences between the early-leafing and late-leafing stands were found. The uniformity of the topographical features suggests, moreover, that there should be none. While considerably more temperature data are needed for this area, the evidence points to the probability that early-leafing and late-leafing colonies of aspen here represent different genetic strains unassociated with observable bole and pruning characters.

Continuous temperature data from June 1 to September 30, 1951, except for two interruptions of four days each, were secured from contiguous colonies of prevernal and late-leafing aspen at Mt. Timpanogos located in the Wasatch Range 30 miles southeast of Salt Lake City. These colonies, occupying mid-altitudinal positions of about 8,000 feet, all showed the morphological differences described earlier, as well as the

FIGURE I

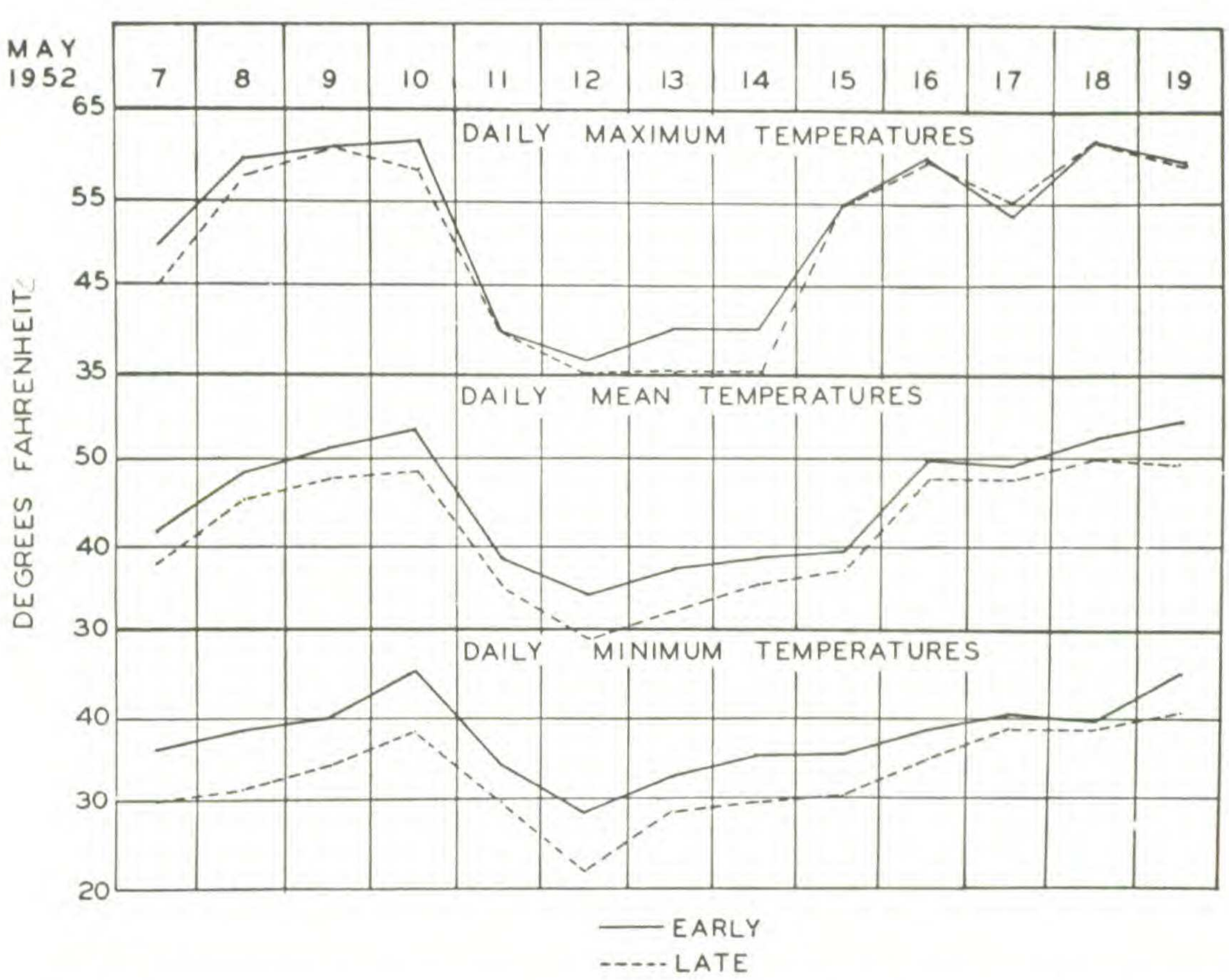

FIG. I. Temperature phenomena of adjacent stands of early- and late-leafing aspen, Stansbury Mountains, Utah. Solid lines early. Broken lines late.

conspicuous differences in leafing time. Figure II represents weekly summaries of the averages of temperature data for two stations each in a pair of contrasting colonies selected for their apparent uniformity of soil and topographical features. Intermittent data from two other pairs of contrasting colonies were also secured throughout the summer. These confirmed the results shown in Figure II.

The data in Figure II reveal that the maximum weekly temperature averaged slightly higher and the minimum temperature averaged slightly lower in the late-leafing colony than in the early-leafing stand, although the mean weekly temperature averages were essentially similar in both. These slight temperature differences may be accounted for by the fact that the late-leafing stand, being slightly more open than the early-leafing colony, allows more sun on the tents by day as well as more effective air circulation by night. However, no aspect of these temperature phenomena is sufficient to account for the great discrepancy of leafing time for these colonies, and the conclusion seems justified that the cause of prevernal leafing lies outside of environmental controls.

FIGURE II

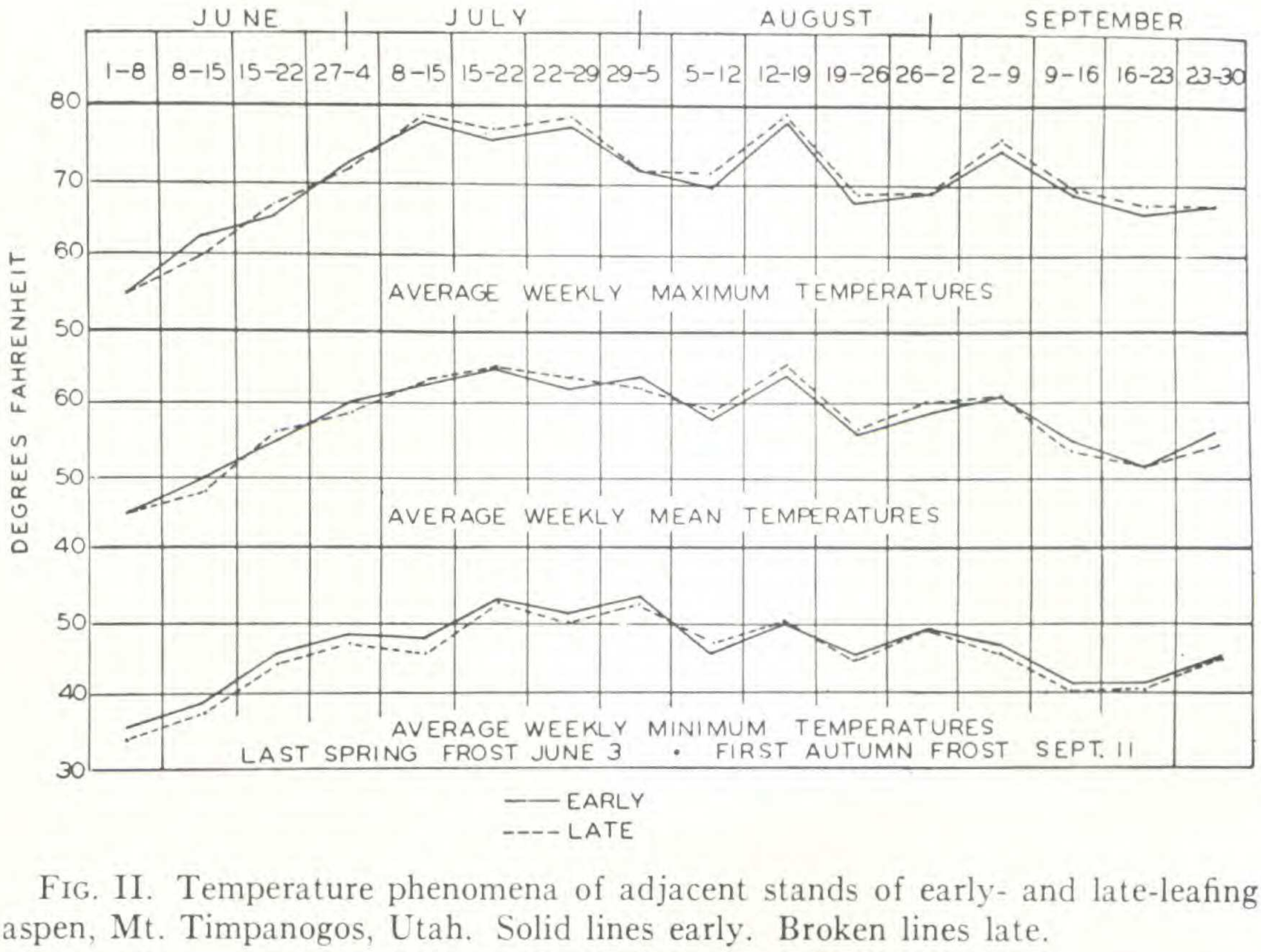

FIG. II. Temperature phenomena of adjacent stands of early- and late-leafing aspen, Mt. Timpanogos, Utah. Solid lines early. Broken lines late.

In order to test the hypothesis that the two distinct leafing forms of aspens possessing recognizable morphological differences at Mt. Timpanogos are true genetic races, other methods of approach seemed desirable: First, the transplanting of aspens from one colony to another, as well as

to a common habitat; second, investigations on the clonal features of the aspen; and third, cytological studies.

TRANSPLANTING EXPERIMENTS

Eight aspen sprouts from three separate pairs of colonies were transplanted in the fall of 1951, thereby introducing into prevernal colonies twelve late-leafing saplings and into late-leafing colonies an equal number of early-leafing saplings. Despite the fact that care was exercised to locate the transplants on the edge of the colonies where competition for light and moisture could be reduced to a minimum, none of the aspen sprouts survived the winter and summer of 1952.

In this experiment it was recognized that several years must elapse before conclusive results might be expected, assuming successful transplantings were possible, because observations have disclosed the fact that aspen sprouts must attain considerable height before they acquire either the morphological characters or the leafing peculiarities of the mature stand. The retarding of the leafing time of the sprouts in prevernal colonies is especially noticeable and may be accounted for by the fact that leafing of the mature trees is generally well advanced before the snow pack has disappeared from the stand. Obviously the close proximity of the snow to the sapling buds has a retarding effect on leafing.

In addition to these transplantings in the field, four saplings from late-leafing aspen stands and four saplings from early-leafing colonies were removed to the University of Utah campus, where previous transplantings of aspen sprouts have proved successful. These transplants were made in late May, 1952, to a favorable situation where nearly uniform factors of soil, water and light were maintained for all saplings.

Three saplings from the late-leafing variety and two from the early survived the summer of 1952 and the winter of 1953. In the spring of 1953 both early-leafing sprouts came into leaf more than two weeks before the late-leafing transplants. Thus the leafing character of the two mountain strains was maintained under totally different environment, and the hypothesis of genetic controls received considerable support.

CLONAL CONNECTIONS OF ASPEN COLONIES

It was assumed that if the present strains of aspen had their origin in seed mutation, contiguous colonies of early- and late-leafing forms should show no clonal connections, although such connections might be expected to exist between trees within the same colony. To determine the nature and extent of aspen clonal connections, at Mt. Timpanogos radioactive phosphorus was employed.*

Selected for radioactive phosphorus treatment was a white-boled, late-leafing tree which occupied a position between closely contiguous colonies of distinct strains of aspen. On one side the branches of this tree inter-

* The writer is indebted to the Research Committee, University of Utah, for supplying the necessary radioactive phosphorus used in this experiment; to Dr. Robert C. Pendleton for labeling the tree; and to Dr. John D. Spikes for monitoring the laboratory specimens.

mingled with those of early-leafing trees and on the other with branches of late-leafing individuals. The nearest bole of the late-leafing variety was 7 feet 6 inches distant, and the nearest bole of the early variety was 6 feet 6 inches. There were six early-leafing trees and seven late-leafing ones within a radius of 17 feet. Near the tree selected for labeling, a trench was excavated exposing the roots, one of which was severed about three feet from the bole. The cut end of this root was inserted into a gallon jar of water containing 40 millicuries of radioactive phosphorus (P–32).

Within 36 hours most of the radioactive phosphorus solution had been absorbed by the tree. The tube of a Geiger counter was placed in a rectangular hole cut breast high in the bark of the labeled tree, thereby exposing the cambium. The counter showed a radioactivity of 60,000 counts per minute. No other tree of either variety in the vicinity of the labeled tree showed radioactivity above background. In subsequent days portions of the roots, cambium, wood and leaves of the labeled tree and of the early- and late-leafing trees surrounding it were removed to the laboratory. These specimens were ashed and tested with a standard scaler provided with a thin-end, window Geiger tube. All ashed samples from the labeled tree gave more than 50,000 counts per minute. No radioactivity above background was found in the samples of any other tree. Excavations around the labeled tree showed that all roots belonging to the labeled tree were radioactive, but that the radioactive substance had not passed to the roots of neighboring trees of either strain.

The results of this experiment are indeed surprising, for they suggest complete separation of the aspen sprouts from the parent clone before or soon after maturity. Considerably more investigation is necessary to establish the clonal characteristics of the aspen.

CYTOLOGICAL TESTS

The field of cytogenetics should offer an interesting and possibly a fruitful approach to the problem of the leafing strains of aspen. So far, however, the writer has encountered perplexing delays in securing suitable tissue for study. Because of the unreliability of aspen seed production, and the major difficulties of securing pollen smears from the remote and snow-bound experimental area, it was assumed that cuttings would provide the most feasible source for securing tissue in active cell division. Numerous greenhouse attempts have been made to root aspen cuttings without a single positive result to date. Additional effort to secure root tips for study is currently in progress.

Positive miscroscopic evidence of chromosome aberrations would, of course, establish the validity of these genetic strains, but negative evidence would not necessarily preclude it, for mutations may be the result of one or a few unobservable gene changes.

DISCUSSION

Whether cytologically demonstrable or not, the fact or the assumption that these readily distinguishable forms of early- and late-leafing aspen

represent mutant strains presents problems of origin and subsequent distribution both interesting and perplexing to the ecologist. For no fact of aspen ecology, in Utah at least, seems more certain than that aspen trees in general, despite occasional abundant viable seed production, reproduce only through vegetative means. They do this because aspen seeds must germinate within a few weeks after ripening in early June. Under present climatic conditions precipitation in Utah is invariably scant and irregular during the summer months. Thus the wide and spotty distribution of aspen throughout Utah today must have been attained under climatic patterns of more abundant and more evenly distributed summer precipitation. Such conditions are postulated by geologists for the Great Basin region during the pluvials associated with the extensive Pleistocene glaciations (1, 2 & 3).

After the onset of the Postpluvial climate in the Great Basin area, which Antevs estimates at approximately 8,000 years ago, it is likely that aspen ceased its reproduction by seeds. Since then migration has been through clonal reproduction only, and exceedingly slow, but sufficient to effect the mergence of many previously separated colonies and to extend the upper altitudinal limits of the aspen belt. Conversely, the increased temperature and lower summer precipitation of the Postpluvial may have caused considerable retreating migration from lower limits of the Pluvial aspen distribution. There are examples of the complete disappearance of aspen colonies at lower elevations during historical times, but grazing influence may have been a contributing cause.

Any proposed hypothesis to explain the origin and present-day distribution of early- and late-leafing aspens must account for the following facts:

1. The predominance of late-leafing forms at low and mid-elevations.
2. The predominance of early-leafing aspen at higher elevations.
3. The widely intermingled colonies of the two forms at mid-elevations, their sharp discontinuity and the purity of their stands.

Assuming that mutations have occurred within the sex cells and therefore have involved successful seedling establishment, it must follow that the mutant strains date back to Pluvial times. Since the altitudinal migration of aspen in Postpluvial times has been mainly upward, and since the late-leafing strain dominates the lower aspen elevations today, the late-leafing form must be the parent type.

It seems obvious that a longer photosynthetic period (upwards of three weeks) acquired by the mutant strains would give them distinct physiological survival advantages over the parent form, particularly at higher elevations where the frost-free period is short, provided, of course, that they also possessed adaptive resistance to lower temperatures. The ability of the early-leafing form to withstand frost in spring is apparent because banks of snow are frequently present beneath the aspen canopy when these trees come into leaf. Temperature records in the early-leafing experimental colony at Mt. Timpanogos, with no snow on the ground in 1951, showed night temperatures of 30° F. or below for a period of approximately

nine hours duration each for June 1, 2 and 3. On the night of June 1, 1951, the minimal temperature of 26° F. prevailed for approximately three hours. The aspen leaves in the early-leafing colony at this time were about one half mature size, while the adjacent late-leafing trees were still in the bud stage.

Whether or not this insensitivity to mild freezing temperature is merely another expression of the same mutation that produced early leafing would be difficult to determine, but certainly the prevernal appearance of aspen leaves would be impossible without this adaptation. That the same degree of frost resistance is not possessed by the late-leafing form is suggested by its apparent inability to invade the upper limits of the aspen belt, by its failure to produce leaves at mid-elevations until the frost period is over and by its habit of dropping leaves earlier in the fall than the early-leafing varieties growing in similar habitats.

At mid-elevations it is apparent that both strains of aspen successfully established seedlings at the close of Pluvial times after these mountain areas had been cleared of the receding ice. It is probable that at lower elevations, high temperature and drought were more limiting as factors of successful aspen establishment than a longer photosynthetic period. Also, suitable sites for aspen were already occupied by the late-leafing parent type. Assuming that neither strain had significant advantage at mid-elevations, the preponderance of seed of the late-leafing strain would account for the dominance of the late-leafing form at mid-elevations today. Clonal reproduction over the centuries of Postpluvial time from trees of these two strains as loci for vegetative migration has, in many instances, brought about the mergence of these two contrasting leafing forms into a single forest stand.

A critical test of this hypothesis awaited the experiment using radioactive phosphorus to trace the clonal relationship of the two strains. It was postulated that a solution of radioactive phosphorus applied to the roots of an aspen of either strain, situated at the line of contact of the diverse colonies, should, according to the hypothesis, pass freely through the root connections to neighboring trees of its own strain, but never to the trees of the opposite strain regardless of their proximity to the labeled tree. The one experiment performed thus far is therefore disappointing as evidence for or against the hypothesis in that it suggests that mature aspen trees in a colony sever their clonal connections.

SUMMARY

1. Almost any aspen forest in early spring in Utah and neighboring states shows sharply discontinuous colonies of trees that attain full leaf two to three weeks earlier than the major stand that surrounds them. The colonies of prevernal aspen are usually small in comparison with the forest as a whole, and in general they are most pronounced at mid-elevations of the aspen belt.

2. Extensive data secured with recording thermographs show that one segment of an aspen forest exhibiting prevernal leafing, is a response to

temperature controls, but that in general the early-leafing colonies of aspen represent distinct genetic strains in which temperature is not a factor.

3. As a rule the leafing habit of the various aspen strains is associated with morphological characters by which they may be identified at all seasons.

4. Saplings of early- and late-leafing strains of aspen transplanted to the University of Utah campus at an elevation of 4,500 feet exhibited the same time difference in leafing as their parent colonies at 7,800 feet.

5. An hypothesis proposed to explain the origin, present distribution and nature of prevernal aspen colonies postulated the following:

(a) Sexual mutations of the late-leafing parent type occurred in Pluvial times.

(b) Migration to and establishment of these strains at higher elevations followed the disappearance of mountain ice and snow packs.

(c) Early-leafing forms dominate the upper limits of the aspen belt because of their longer photosynthetic period and their physiological adaptations to lower temperatures.

(d) Clonal reproduction over the centuries of Postglacial time from seed-established trees as loci for vegetative migration has produced the mergence of these contrasting leafing strains into single forest stands.

UNIVERSITY OF UTAH,
SALT LAKE CITY, UTAH.

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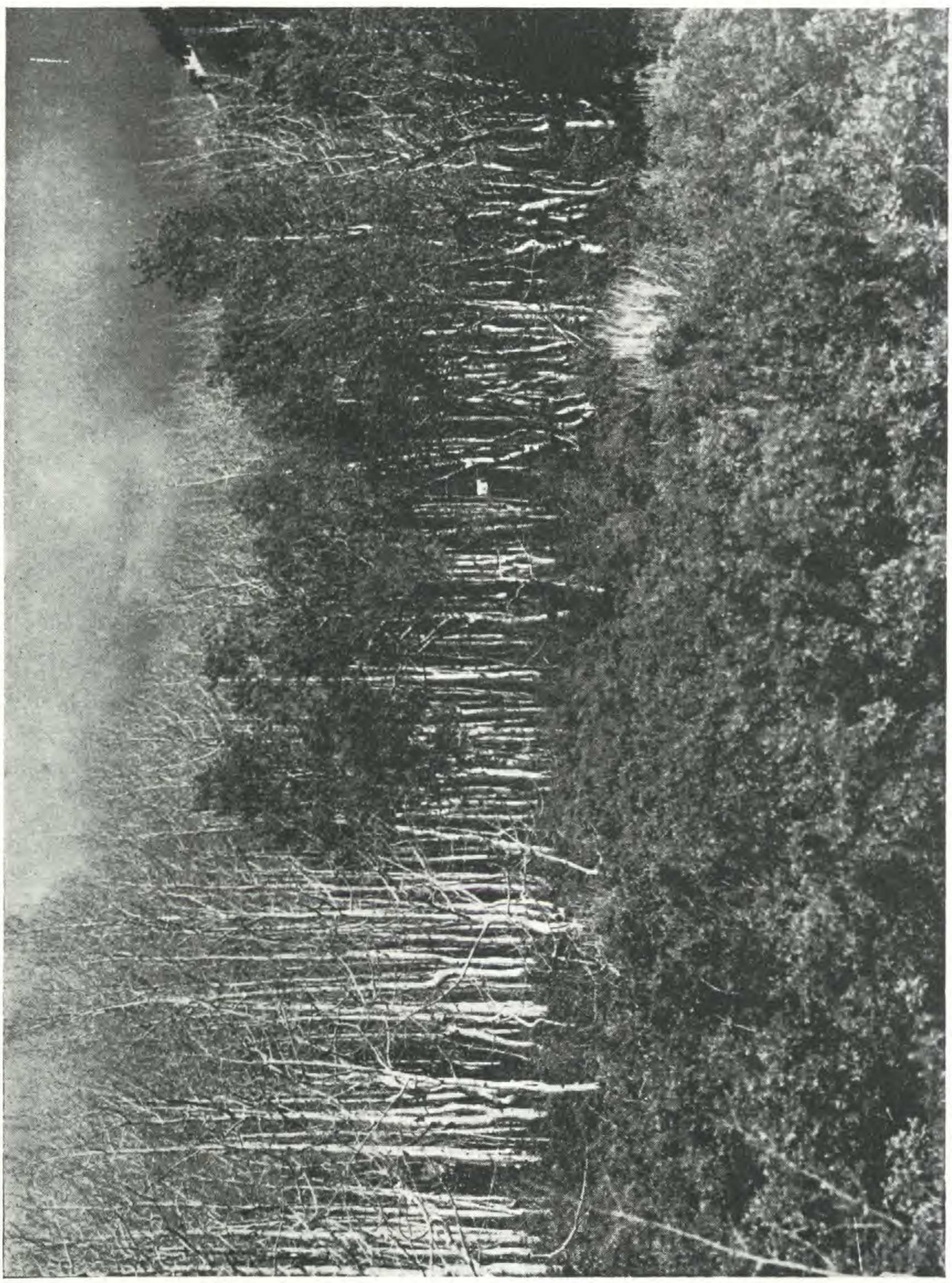
EXPLANATION OF PLATES

PLATE I

Typical stands of early- and late-leafing aspens, mid-elevation (7800 feet). Mt. Timpanogos, Utah. In the right mid-ground is seen the protective tent covering for one of the recording thermographs used to compare atmospheric temperature phenomena of the contiguous aspen strains.

PLATE II

Late-leafing aspens (foreground) have white, well-pruned boles in northern Utah, while the early-leafing forms (background) are yellow-boled and poorly pruned.



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